

# Activity of Superior Colliculus in Behaving Monkey.

## II. Effect of Attention on Neuronal Responses

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IN ALL PREVIOUS studies on visual receptive fields of single neurons (3), including our previous study on the monkey superior colliculus (6), the properties of the cells were studied without regard to the behavioral significance of the visual stimuli. Most animals were anesthetized, paralyzed, or had brain stem transections. Even awake and behaving monkeys were voluntarily fixating a point extraneous to the receptive field of the cell being studied (6).

The awake animal does not treat objects in the visual world uniformly: it responds to some and ignores others. At some point in the brain neurons must reflect not only the external parameters relating to the physical properties of the stimulus, but also the internal parameters relating to whether or not the animal will respond to the stimulus. By altering the response required of a trained animal to a stimulus, we can see if the behavioral significance of the stimulus can affect the response of a neuron with sensory function.

In order to investigate the effect of changing the significance of a stimulus on the response of a sensory neuron, we examined the responses of neurons in the monkey superficial gray and optic layers to visual stimuli under varying behavioral conditions. The presence of a stimulus in the visual field is not sufficient to evoke an eye movement. The monkey must decide that the stimulus deserves further investigation—that is, he must attend to it—and only then will he move his eyes. In the present experiments we trained monkeys to make a saccade to a spot of light under some circumstances and to

ignore the light—that is not to make a saccade to it—under others. We then asked whether or not the response of a neuron to that stimulus was affected when the monkey was going to use the stimulus as the target for a saccade.

We found that the response of many neurons was enhanced when the receptive-field stimulus was the monkey's saccade target. Since we can infer that the monkey attended to the stimulus when he made a saccade to it, the enhancement can be viewed as a neurophysiological event related to the psychological phenomenon of attention.

An abstract of these results has been published previously (5).

### METHODS

The general procedures used for training the monkeys, restraining them, and recording eye movements and single-cell activity have been described in the preceding paper (6).

In these experiments the monkey had been first trained to fixate a spot of light as small as  $0.05^\circ$  in diameter as in the previous experiment (6). When the monkey pressed a bar, the fixation point appeared on a tangent screen in front of him, stayed on for 1–3 sec, and dimmed for 0.5 sec. If the monkey released the bar while the spot was dim, he received a liquid reward. The monkey was sufficiently interested in the fixation point so that if another visual stimulus were flashed elsewhere on the screen during the time the fixation point was on, the monkey did not break fixation to examine the new stimulus. However, when the fixation point went off and another spot of light came on at the same time, the monkey had been trained to make a saccade to the new spot. During some fixations this second spot dimmed, on others it went off and the original fixation point came on again and dimmed. Thus, in these experi-

ments the second spot was used both as a receptive-field stimulus and as a target for a saccade.

Figure 1 outlines the experimental sequence used in the present study. After we isolated a neuron in the superior colliculus, we determined its receptive field while the monkey fixated the fixation point, using a receptive-field stimulus not much larger than the fixation point. Every cell studied in these experiments

was of the type described as pandirectional in the preceding paper (6), and the receptive fields of these cells were all mapped using small spots of light. Figure 1A shows the receptive field of a typical neuron used in the study. The location of the fixation point is labeled FP. The dashed lines indicate the margin of the tangent screen area where the onset of a spot of light evoked an excitatory discharge from the neuron while the monkey fixated the FP. A typical spot used to evoke an excitatory discharge is labeled RF. Every cell in the present study had receptive fields well outside the fovea so that saccades from fixation point to receptive-field stimulus could be detected on the electro-oculogram (EOG) records.

After the receptive field of the cell had been outlined, the experiment was done in two steps. The first step was to pick one point in the receptive field and project a small spot, usually  $0.25^\circ \times 0.25^\circ$ , onto the same point during successive fixations. The response of the unit to this stimulus was then recorded during this period, usually between 10 and 30 trials, in order to establish the neuron's base-line response to a stimulus. Figure 1B shows the animal's eye movements during a typical trial. The animal had started to fixate before the time period shown in the illustrations began. The indicator line in the first trace shows the time when the receptive-field stimulus appeared, and the next two traces are the horizontal and vertical EOG which show no deflection in response to the onset of the stimulus. This experimental condition during which the animal made no eye movement in response to the receptive-field stimulus will be referred to as the no-saccade condition.

The second step was to change the experimental conditions so that the monkey made a saccade to the receptive-field stimulus. If at the same time that the receptive-field stimulus came on the fixation point went off, the monkey made a saccade to fixate the receptive-field stimulus as he had been trained to do. This is shown in Fig. 1C. The bottom two traces show the monkey's saccade, which has a latency of about 250 msec from the disappearance of the fixation point and the onset of the receptive-field stimulus. This series of fixations will be called the saccade condition. Note that in the saccade condition, as shown in Fig. 1C, the receptive-field stimulus before the eye movement occupied exactly the same retinal position as it did in the no-saccade condition. The physical parameters of the stimulus were therefore identical in both conditions; only the behavioral significance changed.

In Fig. 1B and C the indicator line shows

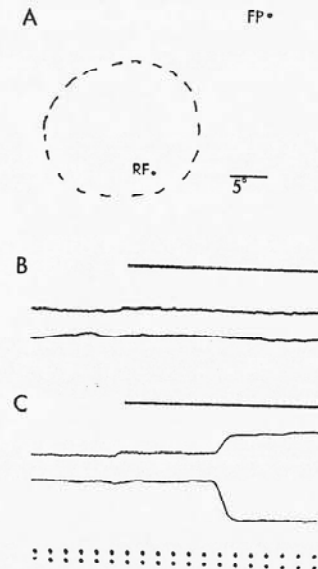


FIG. 1. Sequence of procedures used in experiments. A shows the spatial relations between the spot of light used as the fixation point (FP), and the receptive field (outline by dashed lines) and the spot of light used as the receptive-field stimulus (RF). B shows the onset of the stimulus (upper trace), the horizontal EOG (second trace), and the vertical EOG (third trace) during a fixation under the no-saccade condition. The stimulus indicator shows approximately when the spot of light appeared on the screen. The monkey had begun fixating the fixation point before traces started and continued during the time after the stimulus was turned on. C shows the same traces during the saccade condition. At the indicator trace the receptive-field stimulus came on and the fixation point went out, and about 300 msec later the monkey made a saccade from the fixation point to the receptive-field stimulus as indicated by the deflection in the EOG. The small deflections in the EOG traces occurring simultaneously with the deflection of the stimulus indicator are due to cross talk between channels of the recording system. Rows of dots at the bottom of this and all subsequent figures are time markers, 50 msec between successive dots.

only approximately when the receptive-field stimulus came on; on-response latencies for all the units studied fell into the 40- to 50-msec range described in the preceding paper (6). After each fixation, regardless of whether the response was correct or incorrect, the bar was disconnected for 1-3 sec, and this disconnection was indicated to the monkey by a clicking sound. Experiments were usually done on several cells in the same penetration, and a new penetration was generally started at the beginning of each day.

The location of interesting cells was marked by passing current through the electrode to make an electrolytic lesion. After the experiments were over, the monkey was anesthetized, perfused with saline and 10% formalin in saline, and the brain removed and sectioned.

## RESULTS

The change in cell activity when the receptive-field stimulus became the target for a saccade was studied for 100 neurons in the superficial gray and optic layers of the superior colliculus in four monkeys. Of these 100 cells, 51 showed an enhanced response when the monkey made a saccade to the receptive-field stimulus.

An example of a neuron showing such enhancement is shown in Fig. 2. The indicator line shows when the receptive-field stimulus came on; successive trials are shown on successive lines with each cell discharge and the beginning and end of each line indicated by a dot. In Fig. 2*A*, while the monkey fixated the fixation point, the stimulus came on at a point in the receptive field (no-saccade condition) and there was a weak irregular response. In Fig. 2*B*, as the receptive-field stimulus came on, the fixation point went off and the monkey made a rapid eye movement to the receptive-field stimulus (saccade condition); the cell had a clearer and more consistent response to the stimulus. Note that the eye movement (as shown in Fig. 1*C*) occurred long after the cell's response to the stimulus and therefore did not affect the retinal position of the stimulus. In Fig. 2*C*, as the receptive-field stimulus came on, the fixation point no longer disappeared; the experimental conditions returned to the no-saccade condition as in 2*A*, and the monkey immediately stopped making saccades to the receptive-



FIG. 2. Enhancement of the on-response of a cell to the receptive-field stimulus. The line above the figure indicates approximately when the receptive-field stimulus came on. Each dot represents a cell discharge or the beginning and end of a line. Each horizontal row of dots represents the part of a successive fixation period around the onset of the receptive-field stimulus. In the trials in *A* there was no saccade to the receptive-field stimulus (no-saccade condition), while in *B* the fixation point light went off as the receptive-field stimulus came on (saccade condition) and the cell response was enhanced. *C* again shows the no-saccade condition: the response decreased to the original level. The entire sequence of fixations from *A* through *C* was run without interruption. The receptive-field stimulus was about 10° to the left and below the fixation point.

field stimulus. The enhanced response waned over the next 20 trials, returning to the level that was present during the initial period shown in Fig. 2*A*.

The form of the response enhancement during the saccade condition varied from neuron to neuron, but two general types of enhancement could be distinguished. In the first type, the initial response to the stimulus (the on-response) was more regular and more vigorous in the saccade condition than in the no-saccade condition (as

in Fig. 2). In the second type of response enhancement there was an enhanced response continuing after the initial on-response burst; we refer to this later discharge pattern as the late response. This late response either followed an enhanced on-response (Fig. 3*B*) or appeared independently of any on-response enhancement (Fig. 4*B*). The late response ended when the eye movement to the receptive-field stimulus began, thus moving that stimulus off the receptive field of the cell.

## Response enhancement and eye movement

We have tacitly assumed that the response enhancement is selectively related to eye movements to the receptive field of the cell. However, the possibility remains that this enhancement results from some nonspecific effect related to the effort of making an eye movement—e.g.,

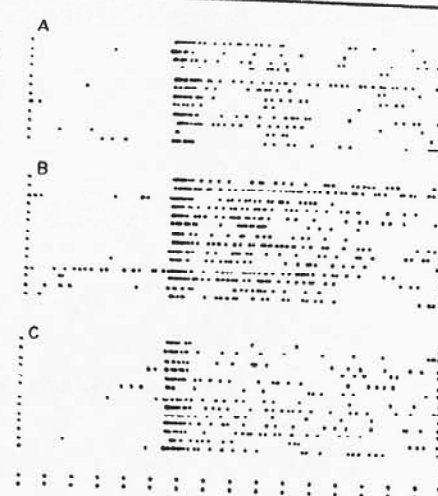


FIG. 4. Late response with saccade condition. No-saccade condition in *A*, saccade in *B*, no-saccade in *C*. Continuous series of fixations with the receptive-field stimulus 8° to the right and below the fixation point.

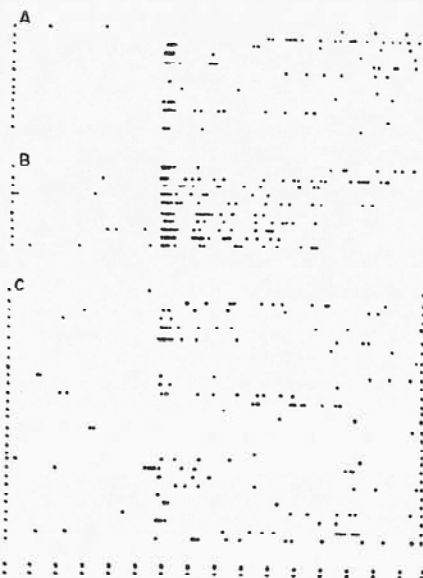


FIG. 3. Enhancement of the on-response and development of a late response with the saccade condition. *A* was the no-saccade condition, *B* the saccade condition, *C* the no-saccade condition again. Fixations from *A* through *C* were consecutive; the receptive-field stimulus was about 17° to the left and above the fixation point.

a central effect such as increased state of arousal, or some peripheral effect such as a pupillary dilation prior to the eye movement. If this were the case, one would expect to see the enhancement in the presence of any saccade comparable in distance to the one required to fixate the receptive-field spot. To examine this question, we presented the monkey with two similar spots of light at the time of disappearance of the fixation point: the stimulus in the receptive field, and a control spot outside the receptive field. The monkey was rewarded for fixating either spot and tended to make a saccade to either one indiscriminately. After the experiment the trials were sorted into saccades to the control spot and saccades to the receptive-field spot. Figure 5 shows the results of such an experiment. In Fig. 5*A* both stimuli came on during the no-saccade condition; in Fig. 5*B* both stimuli came on during the saccade condition, but the trials shown are those in which the monkey made saccades to the control stimulus. There may be marginal enhancement of the late response to the receptive-field stimulus. In Fig. 5*C* both stimuli appeared, but the

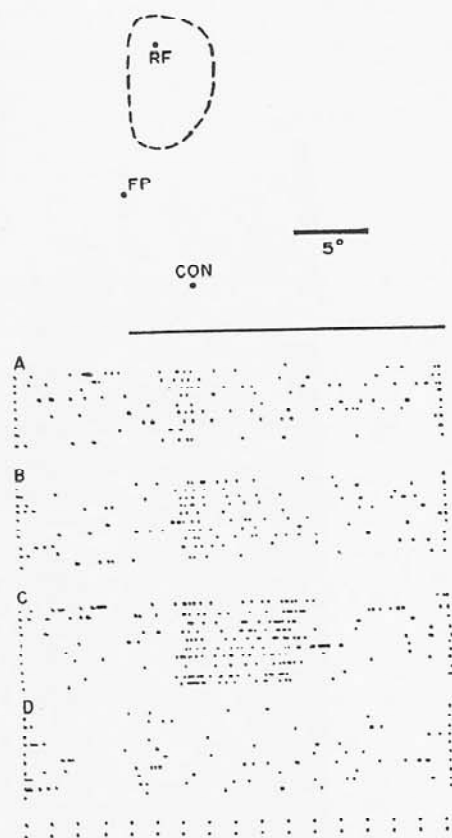


FIG. 5. Selectivity of response enhancement. The drawing shows the location of the receptive-field stimulus (RF) above the fixation point (FP) and a control stimulus (CON) below the fixation point. In *A*, *B*, and *C* the receptive-field and control stimuli both came on at the indicator line. *A* shows the no-saccade condition. In *B* the monkey made a saccade to the control stimulus and in *C* to the receptive-field stimulus. Unlike all other illustrations in this paper, the trials shown in *B* and *C* are not consecutive since the monkey made saccades randomly to one of the two spots in the field, and the trials were separated into groups according to direction of saccade. Within each group responses are shown in serial order. In *D* only the control stimulus came on and the monkey made a saccade to it; trials are consecutive. Cell is one that habituated rapidly, same as cell in Fig. 4.

trials shown are those in which the monkey made saccades to the receptive-field stimulus; there is a marked enhancement of both the early and the late response to the receptive-field stimulus. The enhance-

ment of the cell response to the receptive-field stimulus is related selectively to eye movements made to the receptive-field area and not to eye movements in general.

Whether the possible slight enhancement in response associated with saccades to the control stimulus (Fig. 5*B*) was related just to the occurrence of the eye movement was considered in a subsequent control experiment. The monkey made a saccade to the control stimulus without any stimulus present in the receptive field. There was no response of the unit associated with the eye movement (Fig. 5*D*); the saccade, therefore, had no effect on the activity of the cell when there was no stimulus in its receptive field. There may be, however, a slight nonspecific enhancement of the response to the stimulus associated with an eye movement, and the larger selective enhancement is superimposed on this smaller effect.

The response enhancement before an eye movement depended on the presence of the stimulus; it did not consist of a stimulus response and a separate movement-related response (24). This is shown in Fig. 6. The cell shows a vigorous burst of discharges before an eye movement to a stimulus in its receptive field (Fig. 6*A*), but shows little or no response before an eye movement made in total darkness (Fig. 6*B*).

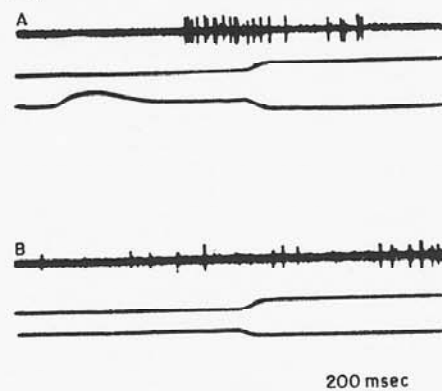


FIG. 6. Comparison of the enhanced cell response occurring before an eye movement made to the receptive-field stimulus (*A*) with the lack of response of the same cell before a similar eye movement made in total darkness (*B*). First EOG trace is horizontal, second is vertical.

Further evidence that the late response is not mechanistically related to the eye movement is provided by a comparison between the temporal relationship of cell response to stimulus onset and the relationship of cell response to eye movement. Figure 7*A* shows the cell shown in Fig. 4 with the display triggered first by the stimulus onset (Fig. 7*A*, 1) and then by the eye movement (Fig. 7*A*, 2). There was no synchrony of the early response to the eye movement, but each late response ended about 50 msec after the saccade. Since the latency of any stimulus effect on cell-discharge pattern would be expected to be 40–50 msec (6), the ending of this late response 50 msec after the saccade would seem likely to result from the motion of the stimulus through the retinal receptive field of the cell as the monkey moved its eyes. In Fig. 7*B*, 1 a weak on-response of the stimulus was followed by a clear late response which is frequently ended in a burst of cell discharges. When these cell discharges were aligned on the eye movement (Fig. 7*B*, 2), no apparent relation existed between the early on-response or the late response and the eye movement. When the late burst came it again followed the eye movement by about 50 msec and it again seemed likely that this burst and pause was an effect secondary to the eye movement rather than a part of the late response.

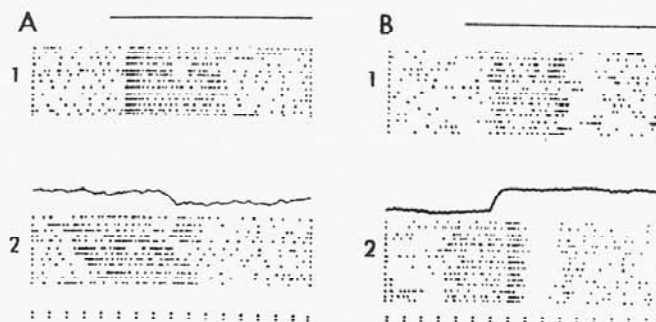


FIG. 7. Comparison of the temporal relationship of cell responses to the receptive-field stimulus and to the eye movement made to the receptive-field stimulus. Responses of two cells are shown in *A* and *B*. The cell response is aligned with the onset of the receptive-field stimulus (shown by indicator line) in the segment labeled 1 and is aligned with the eye movement (located by the sample eye movement) in the segment labeled 2. In *A*, 2 the response ended shortly after the eye movement started, and in *B*, 2 the cell gave a burst of discharges at the same time, and both these responses presumably resulted from the eye movement. The on-response is not well synchronized with the eye movement in *A*, 2 or *B*, 2. Cell in *A* is same as in Fig. 4, cell in *B* is same as in Fig. 5.

The final evidence for the independence of the enhancement from the actual motor act of a successful saccade is provided by looking at the trials just at the beginning and just at the end of a saccade period to see if the enhancement of the cell response necessarily started and stopped in the fixation period in which the monkey made a saccade to the receptive-field stimulus. Figure 8*A* shows cell discharges and eye movements for the transition from the no-saccade to the saccade condition on a trial-by-trial basis for the same cell shown in Fig. 4. Figure 8*A*, 1 shows the last in a series of no-saccade trials with an on-response unaccompanied by an eye movement. Figure 8*A*, 2 shows the first saccade-condition trial. The monkey did not make a saccade to the receptive-field stimulus but instead made a saccade elsewhere (and let go of the bar and missed the reward); there was a late response to the stimulus. In Fig. 8*A*, 3 the monkey made the correct saccade to the receptive-field stimulus and the late response was again clear. This enhancement continued for subsequent trials as the latency for eye movements became shorter (Figs. 8*A*, 4, 5). For this cell, the enhancement was clear on the trial with the correct saccade to the stimulus, and present somewhat on the previous trial. For all the cells studied, the enhance-

ment during the saccade condition was always clear by the time the saccade to the receptive-field stimulus was made correctly, but the enhancement occasionally occurred on the trial before the correct saccade was made.

The end of the same saccade period for the same cell is shown in Fig. 8*B*. Figure 8*B*, 1 shows the last fixation in the saccade

condition with the enhanced cell response and the eye movement. Figure 8*B*, 2 shows the first trial of the no-saccade period; the fixation point no longer went off as the receptive-field stimulus came on, and even on the first trial the monkey stopped making an eye movement to the receptive-field stimulus. This was the case for most trials: when the fixation point no longer

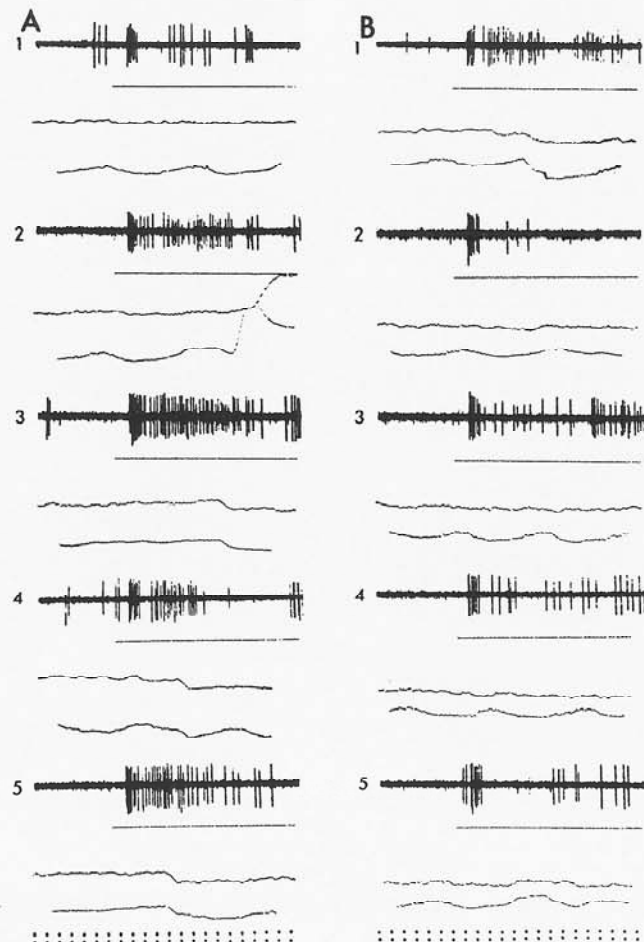


FIG. 8. Relation of response enhancement to eye movement in each successive trial. Same unit as in Fig. 4. In each segment of the figure the indicator for the receptive-field stimulus is below the trace showing cell discharges; upper EOG trace is for horizontal, lower for vertical eye movements. *A*, 1 shows the no-saccade condition while *A*, 2-5 show successive fixations in the saccade condition. The first correct saccade occurred in *A*, 3, as did a clearly enhanced unit response. *B*, 1 is the last trial at the end of the same saccade series shown in *A*. *B*, 2-5 shows the subsequent no-saccade trials; there were no saccades to the receptive-field stimulus but some continuation of the response enhancement. The 4-Hz slow wave on some of the vertical EOG traces is an artifact related to the monkey's sucking on the drinking tube. Same cell as in Fig. 7.

went out, the monkey did not persist in making a saccade to the receptive-field spot. But even though there was no saccade to this receptive-field stimulus, the cell response frequently remained enhanced (a slight response enhancement persisted in Fig. 8*B*, 3, 4). Therefore the enhancement of the response and the occurrence of the eye movement are not tightly locked: enhancement may appear before and continue after the trials where eye movements are seen.

#### *Habituation and response enhancement*

In the saccade condition the enhanced cell response did not habituate but continued without decrement with the repeated stimulus presentations as seen in the periods of 10-20 trials shown in Figs. 2*B*, 3*B*, and 4*B*. The longest we followed a cell in the saccade condition was 80 successive fixations; there was no decrement of the response. For several cells with shorter series of saccade trials slight decreases in response occurred, but the response to the receptive-field stimulus never reverted to the preceding no-saccade level for any cell studied.

After the saccade period ended, the response usually returned to previous levels but at different rates for different neurons. Figure 9 shows a cell which took a particularly long time to habituate. In Fig. 9*A* the cell response had already habituated after a previous saccade period, and this habituation was immediately reversed by institution of the saccade condition (Fig. 9*B*). After return to the no-saccade condition (Fig. 9*C*), the response continued for many trials but returned to the original level by the end of the 59-trial no-saccade period. The response enhancement returned when the saccade condition was reinstated (Fig. 9*D*), indicating that the decrement of response was reversible. The rate of habituation in the no-saccade period also was slower after many saccade trials or after a long series of intermixed saccade and no-saccade trials. Thus, in Fig. 2*C* the response returned to the original level within 15 no-saccade trials, but later in the experiment and after a long series of saccade trials, the response of the same cell did not habituate in 40 trials. In general the enhancement of the on-response habitu-

ated slowly in the subsequent no-saccade condition (as in Figs. 2*C* and 9*C*), while the late response habituated more rapidly:

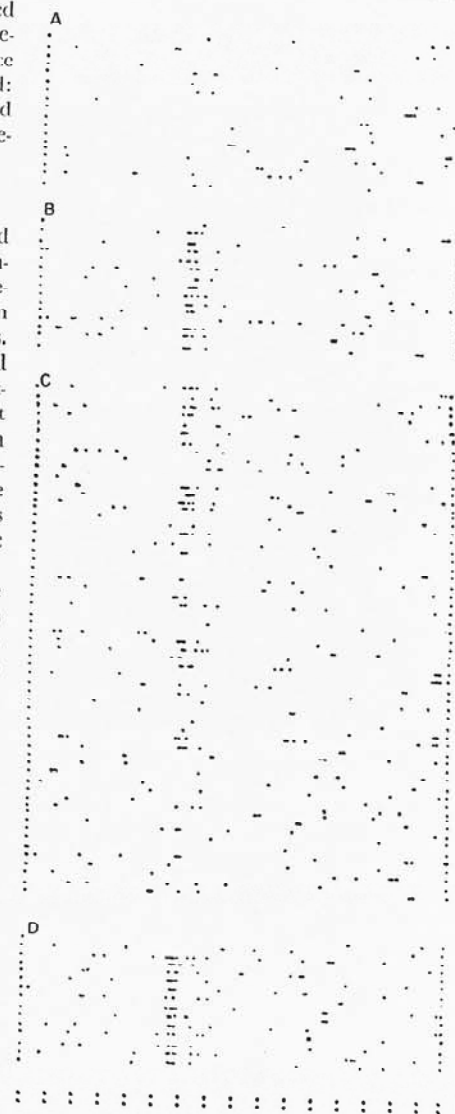


FIG. 9. Slow habituation of on-response enhancement in no-saccade condition. Trials in *A* are done in the no-saccade condition, in *B* in the saccade condition, in *C* in no-saccade condition, and in *D* saccade condition again. Trials were sequential with no interruption; the receptive-field stimulus was about 10° to the left and below the fixation point.

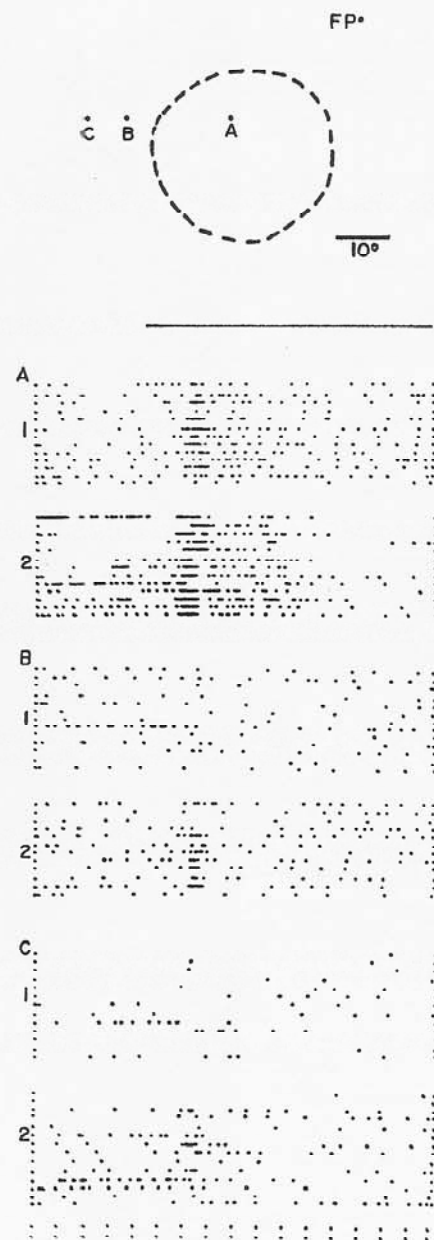


FIG. 10. Expansion of receptive field of a cell under the saccade condition. Point A was in the receptive field mapped while the monkey fixated the fixation point and points B and C were outside the field. Part 1 in each segment shows cell re-

on the first no-saccade trial or within a few no-saccade trials (Figs. 3C, 4C).

#### *Effect of saccade condition on receptive-field size*

The effect of the saccade condition on the cell response to the receptive field stimuli at different points within the receptive field was investigated in 10 cells. A neuron which showed expansion of its receptive-field size is shown in Fig. 10. The receptive field for this cell was mapped while the monkey fixated the fixation point, and is shown by the dashed line (Fig. 10) and the cell response to the receptive-field stimulus at points A, B, and C is shown in the records below. At point A within the receptive field there was an on-response to the stimulus during the no-saccade condition (Fig. 10A, 1), and there were both on-response enhancement and a late response during the saccade condition (Fig. 10A, 2). At point B just outside the mapped receptive field, there was no response to the receptive-field stimulus during the no-saccade condition (Fig. 10B, 1) but an unambiguous response during the saccade condition (Fig. 10B, 2). Further away from the mapped receptive field at point C there was still a slight response to the receptive-field stimulus under the saccade condition (Fig. 10C, 2). Therefore, for this cell there was an expansion of one edge of the visual receptive field by about  $10^\circ$ . Four cells studied showed this slight expansion of receptive-field size.

The remaining six neurons studied showed no change in the size of their receptive fields under the saccade condition, but several did show a reversal of the attenuation of response at the borders of the receptive field. Such a cell response is shown in Fig. 11. The receptive-field area was again mapped while the monkey looked at

sponses occurring in the no-saccade condition; part 2 in saccade condition. The cell responded clearly at B and slightly at C during the saccade condition. Experiments were not done in the order shown; the cell showed rapid habituation so that one enhancement did not affect the cell response in a subsequent no-saccade period.

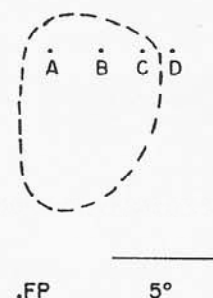


FIG. 11. Enhancement of cell response to receptive-field stimulus within but not beyond the receptive field. Records for each receptive-field

the fixation point. Whereas the initial on-response decreased at points nearer to the edge of the receptive field in both saccade (two of each segment of Fig. 11) and no-saccade condition (one of each segment of Fig. 11), the late response was enhanced in the saccade condition to about the same degree in all three locations. For point D outside the receptive field, there was no response to the stimulus in either case. Thus the effect of the saccade condition in this type of neuron seemed to be an equalization of the response within the various parts of the receptive field rather than an expansion of the receptive field.

#### *Independence of late response from on-response*

All of the cells had an on-response to the receptive-field stimulus, whether or not this response was enhanced during the saccade condition. To see if the late response could be separated from this on-response, we left the stimulus on all the time in certain trials to eliminate the on-response. In Fig. 12A the receptive-field stimulus came on under the no-saccade condition and in Fig. 12B under the saccade condition; there was a late response in Fig. 12B. In Fig. 12C the receptive-field stimulus was left on all the time, but the monkey still made a saccade to it when the fixation point disappeared. Although there was no on-response as in Fig. 12A and B, there was a late response as in Fig. 12B. If the stimulus remained on all the time but under the no-saccade condition (Fig. 12D), there was no response at all, early or late. Thus the late response did occur independently of the on-response. The time of onset of the late response in four cells so

stimulus point (A-D) shown on the receptive-field map are for the no-saccade condition (1) and then the saccade condition (2). The late response was enhanced within the receptive field (A-C) but not outside the field (D). The no-saccade then saccade sequence was continuous for each point, but points were not done in the order shown. The cell response enhancement habituated rapidly in the no-saccade condition so that there was no carryover of a saccade period effect at one point to a no-saccade period at the next point. The late burst response (in B, 2 and C, 2) came after the eye movement. Same cell as in Fig. 7B.

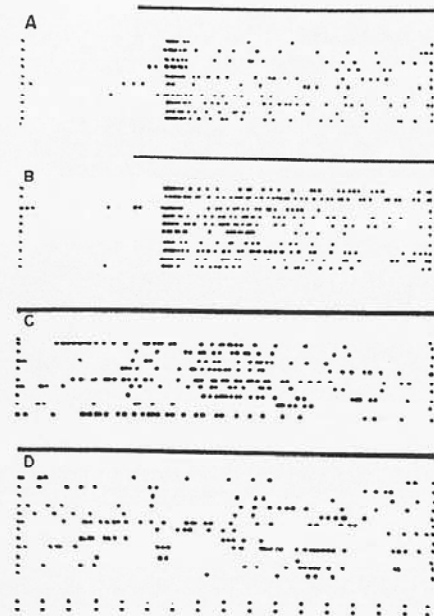


FIG. 12. Separation of early and late response. In *A* the receptive-field stimulus came on under the no-saccade condition, while in *B* it came on under the saccade condition. In *C* the saccade condition continued but the receptive-field stimulus was on all the time so there was no on-response, just a late response. Section *D* was the no-saccade condition with the receptive-field stimulus on all the time. Segments of the experiment were not done in the order shown. Same cell as in Fig. 4.

tested was 50–75 msec after the on-response would have occurred.

#### *Relation of enhancement to receptive-field characteristics*

We found no difference between cells showing enhancement and the other half that did not with respect to the following variables: *a*) size of the receptive field, *b*) distance of the receptive field from the fixation point, *c*) presence of an inhibitory surround, *d*) preference for moving or stationary stimuli, *e*) sequence in penetration, *f*) previous experience with the attention task during the same experimental day, *g*) latency of on-response.

#### DISCUSSION

In these experiments we showed that the response properties of neurons in the

superior colliculus of the rhesus monkey were affected not only by the physical parameters of the stimulus used to excite the cells, but also by the behavioral importance that the stimulus had for the monkey. This phenomenon was demonstrated as an enhancement of cell response when the animal was going to make a saccade to fixate the stimulus, but it was apparent that the enhancement was not the result of some artifact associated with eye movement. It could not have been related to the retinal effects of the eye movement; it could not have been due to some general arousal effect related to performing the eye-movement task; and it was not related to the actual eye movement itself, as opposed to the activity of movement-related cells in the intermediate layers (24). The effect seemed related only to the fact that the monkey was going to use the stimulus in the receptive field.

We conclude that the response enhancement does not result from these factors related to eye movement, but instead seems likely to arise from some central input to the visual system which is involved in selecting out those stimuli which the animal uses for behavior from those stimuli which it does not. We have studied the effects of this central input in the superior colliculus, but we do not know whether the enhancement arises in the colliculus or at some point afferent to the colliculus. Anatomical evidence indicates that the rhesus monkey superior colliculus receives visual input both directly from the retina and indirectly from the occipital cortex (23), and the enhancement could occur in either pathway and still show up as enhancement of response in the superior colliculus. If the central input impinges directly on the superior colliculus, the enhancement could result from activity in one of the many areas that project to the superior colliculus: frontal, occipital, inferotemporal cortex (15), and brain stem reticular formation (in the cat, ref 17).

We also do not know exactly when in the saccade period this central input first acts. Since the late response often occurs on the first trial of a saccade series, and always when the monkey makes the correct eye movement, the central input must act

with a latency no greater than the latency of the late response—about 100 msec. Whether the on-response is ever enhanced for the first trial is not clear from our data. One can usually find a single response in the no-saccade period that looks enhanced, and the effect only becomes clear in the aggregate comparison between the saccade and no-saccade series.

There have been other demonstrations that nonvisual stimuli could affect the receptive-field properties of neurons in the visual system. Weingarten and Spinelli (22) showed that clicks and shocks could augment the response of cat retinal ganglion cells to visual stimuli, and also increase the cell's receptive-field size. Godfraind and Meulders (4) demonstrated similar effects of somatosensory stimulation on lateral geniculate neurons in the unanesthetized cat. This effect was dependent on an intact mesencephalic reticular formation and could be duplicated by reticular stimulation. Bartlett et al. (1) reported that the receptive-field size of squirrel monkey striate cortex neurons could be increased by reticular stimulation. The major difference between these studies and ours lies in our demonstration that the enhancement is behaviorally controlled and specific to the receptive-field area rather than the result of general arousal elicited by a loud click, a shock to the animal, or a pulse train to the mesencephalic reticular formation.

#### *Habituation and adaptation*

The response enhancement that we demonstrate when the monkey makes a saccade to a receptive-field stimulus can be viewed as a dishabituation of a response. Habituation to a stimulus is well defined: it is the decrease in response to repeated stimulation which can be returned to its original level—dishabituated—by changing the context in which the stimulus is given (20). In the superior colliculus such habituation of single-cell responses has been demonstrated in the rabbit optic tectum (12) and in the superior colliculus of the cat (16, 19, 21). In the present experiments when the monkey generated a saccade to the stimulus, the response was enhanced and stayed enhanced with only slight evi-

dence of habituation. At the end of each saccade period when the stimulus was repeatedly presented with no saccade to it, marked habituation of cell response occurred. This probably explains why in our previous study of receptive fields in the superior colliculus (6) we saw no habituation; the monkeys were never making saccades to the receptive-field stimulus and the responses of cells to the stimulus had already habituated and could show no further habituation with repeated stimulation. The response may be enhanced by reintroducing the saccade condition; the context of the stimulus is therefore changed and the enhanced cell response accompanying this change could be referred to as a dishabituation.

The late enhancement of response may also be viewed as a reversal of the process of adaptation of a neuron to a single stimulus. In contrast to habituation, which occurs to repeated stimulus presentations, adaptation is the decrement of response that occurs while a stimulus is on. The superior colliculus neurons studied are frequently phasically responding neurons; they respond to the onset and offset of a spot of light, but show adaptation as long as the light is on. The late enhancement of response may be regarded as a reversal of this adaptation since the response of the cell to the spot of light is extended in the saccade condition beyond the duration of the visual on-response. In the experiment (Fig. 12) where the stimulus remained on all the time, the response to the stimulus had clearly adapted before the fixation started, yet when the animal decided to fixate the stimulus the neuron gave a renewed burst before the eye movement.

Both types of response decrement—the habituation to repeated presentations of a given stimulus and the adaptation to a single presentation of the stimulus—are in this case related to the behavior of the animal, perhaps as a mechanism to screen unwanted sensory information from the higher centers of the nervous system. The mechanism clearly exists to reverse this decrement in response to a stimulus when and if the information becomes important to the monkey, that is, when the monkey pays attention to the stimulus.

Attention, therefore, reverses decrement in response, and attention and habituation are reciprocally related. A possible relationship between the mechanism of habituation and the phenomenon of attention has recently been suggested by Horn (11).

#### *Attention and response enhancement*

The specific enhancement of behaviorally important sensory input that we have demonstrated in single visual neurons is reminiscent of the phenomenon of attention long discussed in the psychological literature. In 1890 James (14) wrote, "Everyone knows what attention is. It is the taking possession of the mind, in clear and vivid form, of one out of what seem several simultaneous possible objects or trains of thought. Focalization, concentration of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others . . ." The modern consensus of the meaning of attention has not strayed far from James' summary. The view that there is a process of attention which allows the nervous system to handle preferentially some sensory inputs which are important to the animal is found in the approaches of Pavlov (18), Hebb (7), and Berlyne (2), among others.

Electrophysiological changes in the brain have been demonstrated during attention by a number of investigators. Cortical evoked responses to flash were diminished when a cat looked actively at a mouse outside the flash zone (10). Somatosensory evoked responses were diminished when a cat was occupied with a can of sardines (9) (for a review of this literature cf. Hernandez-Peon, ref 8). Some single units in the auditory cortex of cat were found to respond only when the cat seemed to attend to the stimulus (13).

These previous results clearly demonstrate beyond doubt that a neurophysiological change occurs during attention. We have tried to extend these results by more closely examining what this change is. In our experiments we combined two factors: 1) we recorded single-cell responses from cells with clearly identified receptive fields in order to permit easy interpretation of the origin of any physiological change, and 2) we controlled the physical properties

of the stimulus so that only its behavioral significance changed. By doing this we have been able to show in what way the cellular change is related to attention: a selective enhancement of the response of some neurons to the important stimulus.

The enhancement might provide a powerful mechanism for affecting the nervous system at a synaptic level. When the response evoked by a stimulus in a neuron is facilitated, the response—and hence the stimulus—would have a greater effect on a postsynaptic cell than a nonenhanced response evoked by a similar stimulus. This stimulus would preferentially influence the workings of the brain—for example, it would be more likely to lead to a motor response, or it could present more information that could be stored as a memory trace. The more enhancement associated with a stimulus, the greater effect that stimulus would have on the nervous system. The enhancement of responses in many similar neurons could be the effect of the mechanism which on the psychological level is the phenomenon of attention.

#### *Problems in study of attention*

Our experiments on the awake monkey share a problem with previous studies that is inherent in the study of a subjective phenomenon such as attention. We can assume that when the monkey makes a saccade to the stimulus he is attending to it. But in order to say that the enhancement of the response is due to the monkey's attention, we must also say that the lack of enhancement in the no-saccade condition is due to the monkey's not attending, and that the waning of the response in the second no-saccade period is due to the waning of the monkey's attention. This, of course, we cannot do since we cannot differentiate between the monkey's not attending to the receptive-field stimulus in the no-saccade condition and his attending to it but deciding not to fixate it. When an animal is attending can therefore only be estimated rather than determined, and the accuracy of the estimation depends on how close one can correlate the monkey's intention to fixate a target—which, post hoc, we can measure—to his attention to the target, which we cannot.

A second problem in the study of the neurophysiological basis of attention is that this unitary behavioral concept may not have a single physiological mechanism. We have described a phenomenon—the enhancement of a response to a stimulus when that stimulus is used by the monkey as data for an obvious voluntary act—and this condition clearly fits the description of attention. But we have performed our experiments in a very constrained manner: we have measured changes in the response to an object located extrafoveally when it is the target for an eye movement. The attention associated with the analysis of complex visual stimuli may be totally different. For example, once an animal fixates an object to permit the finer analysis possible with the fovea, it is still paying attention to the object. The centers, presumably cortical, related to this kind of vision may show changes during fixation but not at all before eye movements. Similarly, auditory and somatosensory attention may stem from excitation of totally different neural systems.

The attention effect we are considering may be also specifically related to the role of the colliculus in the visual guidance of eye movements. While the response enhancement is not obligately related to eye movements, the enhancement might still be related to the neural apparatus involved in preparation for an eye movement. While the on-response enhancement is completely independent of eye movements, the late response is more closely related to eye movements: it can occur independently of the on-response; it ceases more rapidly when eye movements stop after a saccade series; it is closer in time to the occurrence of eye movement. In addition other cells just slightly deeper in the colliculus discharge before eye movements regardless of the stimulus evoking them, and these cells are the subject of the following paper (24).

#### SUMMARY

The receptive fields of 100 cells in the superior colliculi of four monkeys were determined while the monkeys fixated a point of light. After the receptive field of each cell was determined by using stationary spots of light, the first step was to establish

a base-line level of response to a spot of light at a particular point in the receptive field during successive fixations. The second step was to see if the response of the cell changed when the fixation point went off as the receptive-field stimulus came on and the monkey made a saccade to this stimulus. In the time between the onset of the stimulus and the saccade to it (at least 200 msec), the stimulus in the receptive field did not change its physical characteristics, only its significance to the monkey.

About half the cells studied showed an enhanced response to the receptive-field stimulus when the monkey made a saccade to it. The enhancement was a more regular and vigorous on-response in some cells, a late response in the period following the on-response in other cells, or an enhancement consisting of both components in other cells.

The response enhancement was selective. The response was clearly enhanced when the stimulus was the target of a saccade, but it was only slightly altered when the eye made saccades to points in the visual field outside the receptive field. The eye movement to the stimulus also was not required for the enhancement to occur; the enhancement sometimes occurred on a trial before the monkey made his first successful saccade to the receptive-field stimulus and often lingered after the end of a saccade period when no more saccades were made to the stimulus.

During the saccade condition the response showed little habituation. After the saccade period ended the enhanced response habituated over a number of trials—as long as 30–40 trials for the on-response enhancement but within a few trials for the late enhancement. Therefore, when the monkey attended to the receptive-field stimulus by using it as the target of a saccade, the response of the cell to the stimulus did not habituate; when the monkey stopped attending to it, habituation of the cell response to the stimulus began.

The response enhancement was different at different points in the receptive field. For some cells the receptive-field size was increased slightly in the saccade condition. For other cells the receptive-field size was not increased but the response within the

receptive field was equalized so that the response to stimuli at the periphery became equal to that in the center of the field.

We conclude that the enhancement of response to a stimulus results from some central input to the visual system which selects out those stimuli which the animal uses for behavior from those which it does not use. When the discharge evoked in a neuron by a stimulus in one area of the visual field is enhanced, the discharge would have a greater effect on a post-synaptic cell than the nonenhanced dis-

charge evoked by a similar stimulus in another part of the field. The information carried by the enhanced response is likely to be transmitted more reliably to higher levels of the nervous system. The more enhancement associated with a stimulus, the more influence that stimulus would have on the nervous system. We suggest that this enhancement of response in many neurons is the effect of the mechanism which on the psychological level is the phenomenon of attention.

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## Activity of Superior Colliculus in Behaving Monkey.

### III. Cells Discharging Before Eye Movements

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CLINICAL CORRELATIONS (13) and stimulation studies beginning in the last century (1, 4, 12, 22, 28) have provided the evidence for the view that the superior colliculus is involved in the neural generation of eye movements. Physiological studies have concentrated on sensory input to the colliculus, and it has been established that cells in the superficial gray and optic layers of the rhesus monkey superior colliculus have well-defined visual receptive fields (10, 15, 24). The response of roughly half of these cells is markedly enhanced by the monkey's intention to use the stimulus falling in the receptive field of the cell as the target of a saccade, but this enhancement depends on the visual stimulus; in the absence of visual stimuli these cells lose their striking activity before eye movements (11). On the other hand, cells in the intermediate gray and white layers of the colliculus do discharge before saccadic eye movements of specific distance and direction, even in total darkness (24, 30). This report describes the properties of these cells.

A brief report (30) and an abstract (8) of some of these results have been presented previously.

# METHODS

The general behavioral and physiological methods used were the same as described in the two preceding papers in this series (10, 11).

Cells in these experiments were studied under two conditions. First, whether or not the cell had a visual receptive field was determined while the monkey fixated a small spot of light (as in the first paper of this series, ref 10). Second, the monkey was induced to make a saccade or tracking eye movement. A saccade was

produced when the fixation point went off and a second point came on and became the fixation point (11). A tracking eye movement was produced by moving the fixation point in a smooth arc as long as 20°. This was done at speeds ranging from 5 to 125°/sec by reflecting the fixation point off a front-silvered mirror and by applying a ramp waveform to the galvanometer on which the mirror was mounted.

Lateral rectus electromyograms were made using chronically implanted ball electrodes placed on Tenon's capsule through a hole drilled in the squamous portion of the parietal bone. The presence of the small EMG electrode had no measurable effect on the velocity or frequency of eye movements.

Points in a microelectrode penetration where interesting cells were recorded were marked by an electrolytic lesion and located on histological sections.

# RESULTS

In eight monkeys, 70 cells were recorded that gave a burst of cell discharge preceding saccadic eye movements. Electrolytic lesions made through the recording electrode at the site of these cells were located primarily in the intermediate gray and white layers of the superior colliculus with a few points in the deep gray layer. Figure 1 shows one of these lesions that was located at the edge of the intermediate gray layer.

## Cell activity and eye movement

The superior colliculus neurons described in this study all increased their rate of discharge before eye movements of specific direction and distance. The time of onset of the burst varied from cell to cell. Some neurons clearly increased their rate of discharge as long as 200-300 msec before the EOG deflection, others only 30-50 msec before the EOG deflection. Since the cell

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